Ghosts and Orphans

Madagascar's Vanishing Ecosystems

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Introduction: Ghosts and Orphans

Nineteenth century naturalist-explorer Alfred Grandidier was perhaps the first European to gaze upon the ghost bones of Madagascar. The Malagasy knew them well: some belonged to fierce but stupid birds with eggs large enough to hatch a human infant; others belonged to ogres that could be rendered helpless and unable to move when marooned on smooth rocky surfaces. Still others belonged to ferocious, cow-like creatures that might charge unsuspecting humans from a distance, spraying urine and making minced meat out of those who failed to escape. These killer cows might take refuge in crater lakes or water holes; they might steal corn at dawn but retreat into their aqueous abodes when pursued by vigilant farmers (Raybaud, 1902). They had many names, including "omby rano" (water cows), "tsy-aomby-aomby", or "song-aomby" (literally, the "not-cow-cow" or the "cow that isn't a cow"; see Ferrand, 1893; Godfrey, 1986; Burney and Ramilisonina, 1998).

Grandidier was fascinated by accounts of these creatures, and he made a point of inquiring about them wherever he traveled. A village headman whom he met in 1868 at Ambolisatra (southwest Madagascar) was more than obliging (Mantaux, 1971). He led Grandidier to a marsh where he knew that bones of the "song-aomby" could be had. Barefoot and sporting pants cut at the knees, Grandidier ventured into the muck, delicately feeling for treasures beneath his toes. His first prize was an enormous femur of an elephant bird – previously known only through its 8-liter eggs. There were indeed bones of the song-aomby – Madagascar's pygmy hippopotamus. And there was more, much more, including bones of some gigantic lemurs.

The word "lemures" means ghosts, specters, or creatures of the night. Linnaeus (1758) gave it to the ring-tailed lemur – ironically one of the relatively few diurnal species of living lemur. The bones of the giant lemurs are ghosts of

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a different ilk – evolution's true phantoms. Giant lemurs and associated "megafauna" disappeared during the last wave of Quaternary extinctions. They suffered a slow but inexorable decline beginning soon after the first human colonists arrived (around 2,300 years ago) and continuing into the European (or historic) period (Simons et al., 1995a; Simons, 1997; Burney, 1999, 2005; Perez et al., 2003; Burney et al., 2004). Indeed, there is ethnohistoric evidence of megafaunal survival well into the 19th or 20th centuries AD (Godfrey, 1986; Burney and Ramilisonina, 1998; Burney et al., 2004).

In 1982, Daniel Janzen and Paul Martin published a landmark article in Science magazine. Following the lead provided by Stan Temple's research on plant-animal mutualism in Mauritius (1977), Janzen and Martin argued that human-induced megafaunal extinctions in the late Quaternary had left numerous plants effectively orphaned – i.e., lacking important agents of seed dispersal. Their focus was the megafaunal extinctions in Central America 10,000 years ago, hence their title, "Neotropical anachronisms: the fruits the gomphotheres ate." Redford's (1992) "The empty forest" expands on the same theme, as does Barlow's (2000) semipopular book, "The Ghosts of Evolution: Nonsensical Fruit, Missing Partners, and Other Ecological Anachronisms." Richard and Dewar (1991: 167) were among the first to raise the question for Madagascar, proclaiming that "Conservation will not work if forests are protected but lack the fauna needed to ensure their persistence." More recently, aspects of this problem have been addressed by Dransfield and Beentje (1995a, b), Baum (1995, 2003), Ganzhorn et al. (1999) and Birkinshaw (2001), among others. If orphaned plants can survive 10,000 years after the extinction of their partners in Central America, they can certainly survive the few hundred years (or less) since the last of the megafaunal extinctions in Madagascar.

Our task in this chapter is to identify Madagascar's ghosts and orphans. Which of Madagascar's surviving plants are anachronistic, and who are their missing partners? Were some of those partners giant lemurs, and can we identify likely candidates? Can our current knowledge of life history profiles and trophic adaptations of giant lemurs help us in this endeavor?

The Paleontologists' Toolkit

Reconstructing Life Ways of Extinct Species

Paleontologists have the tools to resurrect the ghosts, at least in virtual reality (Jungers et al., 2002; Godfrey et al., 2006a, b). Knowledge of the extinct lemurs of Madagascar has grown rapidly over the past several decades, due in large part to the success of Elwyn Simons in forging a new era of paleontological discovery there (Simons et al., 1990; Simons, 1997; Fig. 1). Simons's expeditions resulted in the discovery of previously unknown skeletal elements belonging to recognized species, and several entirely new species (Godfrey et al., 1990;

Fig. 1 Elwyn Simons, 1988, searching for subfossil lemur bones at Antsiroandoha Cave, Ankarana Massif (northern Madagascar). This was the year of our discovery of the type specimens of the sloth lemur, *Babakotia radofilai*

Simons et al., 1995b). They also resulted in the discovery of virtually whole hands and feet of giant lemurs (Hamrick et al., 2000; Jungers et al., 2005). Long-standing errors of taxonomic attribution have now been corrected (e.g., Wunderlich et al., 1996; Godfrey et al., 1997a; Godfrey and Jungers, 2002; Godfrey et al., 2006c). And, with the discovery of new specimens of immature individuals, we have been able to embrace a new challenge: reconstructing the life history profiles of the giant lemurs.

Life history can be thought of as a set of adaptations that governs the allocation of an organism's energy towards growth, maintenance, reproduction, etc., played out within an ecological context. It is described by such milestones as gestation length, dental and somatic growth rates, weaning age, the ontogeny of ecological independence, age at first reproduction, and so on. Life history features do not fossilize and therefore cannot be examined directly in extinct species. However, microstructural analysis of teeth provides a lens through which life history parameters of extinct species can be observed. Molar crown formation times (CFTs) can be measured as can dental precocity at birth, and life history parameters such as age at M1 emergence and even weaning can be estimated (assuming they relate in a simple manner to age at crown completion). The specific methods of analysis are reviewed elsewhere (see, for example, Bromage, 1987; Beynon et al., 1991; Dean et al., 1993; Schwartz et al., 2002). Chronologies for the development of the entire molar row are now available for *Archaeolemur* and *Palaeopropithecus*; partial molar chronologies are available

for *Megaladapis* (first two molars) and *Hadropithecus* (second molar only) (Schwartz et al., 2002, 2005, 2007; Godfrey et al., 2005, 2006c); additional work on *Mesopropithecus* and *Babakotia* is in progress.

Reconstructing Diets

Tools for reconstructing diet in extinct primates are also diverse, and include comparative analysis of dental morphology, craniofacial architecture, dental microwear, stable isotopes, and trace elements (Tattersall, 1973; Kay, 1975, 1984; Ungar, 1998; Jungers et al., 2002; Rafferty et al., 2002; Burney et al., 2004; Godfrey et al., 2004). Various levels of magnification, from 35x (low magnification stereomicroscopy) to 500x (scanning electron microscopy), have been used in the interpretation of dental microwear of subfossil lemurs (Rafferty et al., 2002; Godfrey et al., 2004; Semprebon et al., 2004). A study using confocal microscopy is in progress (Scott et al., 2007; for the method, see Ungar et al., 2003). Only preliminary stable carbon isotope data ($\delta^{13}C$) are available (see especially Burney et al., 2004); additional research in this realm is also in progress (Crowley et al., 2007). Trace elements have yet to be studied. Table 1 summarizes these data for extinct lemurs from southern Madagascar, thus controlling for variation in abiotic factors (such as climate).

Brains and Body Size

We have measured the cranial capacities of subfossil lemurs, including representatives of all known genera (except for *Daubentonia robusta*, which is unknown cranially). Elsewhere in this volume, we estimate body masses for these same extinct taxa (Jungers et al., 2008), so we can now briefly consider the relationship between body size and brain size in subfosssil lemurs (also see Jungers, 1999), within a comparative context of living strepsirrhines (37 species) and nonhuman anthropoid primates (43 species, sexes plotted separately for dimorphic species) (Fig. 2). Nonparametric (LOESS) lines are plotted for each infraorder in ln–ln space, and the extinct lemurs are enclosed in a convex polygon. The well-known separation ("grade effect" = clade effect) between living strepsirrhine and anthropoid primates (Stephan et al., 1977, 1981; Martin, 1990) is readily observed, and this separation is increased at the larger body masses of subfossil lemurs (all of whom exceed 10 kg). The apparent curvature or kink created by the addition of the giant lemurs indicates that allometric scaling of brain size in strepsirrhines is more complex than linear; regardless, most of the subfossils are much less encephalized than size-matched anthropoids.

Table 1 Dietary inferences for extinct lemurs from southern Madagascar*

Taxon	$\delta^{13}C$ values	Primate species with most similar microwear profiles	Additional observations	Inferred diet
Palaeopropithecus ingens	−19.0, −21.0, −20.6	*Propithecus verreauxi*, *Indri indri*, *Mesopropithecus globiceps*, *Macaca fascicularis*	High shearing quotient suggests that shearing leaves is important, as in sifakas.	Mixed fruit and foliage (with seed processing). Stable carbon isotopes suggest mainly C3 plant foods.
Mesopropithecus globiceps	−15.8, −19.3, −20.3,	*Indri indri, Palaeopropithecus ingens, Propithecus verreauxi, Macaca fascicularis*	High shearing quotient suggests that shearing leaves is important, as in sifakas.	Mixed fruit and foliage (with seed processing). Stable carbon isotopes suggest mainly C3 plant foods.
Daubentonia robusta	−16.3	[No known molars]	Incisors and postcranial skeleton reveal trophic adaptations similar to those of living aye-ayes.	Omnivore, hard-object processor. Stable carbon isotopes suggest mainly C3 plant foods.
Pachylemur insignis	−20.2, −20.6	*Eulemur collaris, Lemur catta, Pachylemur jullyi, Eulemur rubriventer, Varecia variegata*	Pattern of enamel erosion comparable to that observed in other lemurids, such as *Lemur catta*	Mixed fruit and foliage (without seed processing). Stable carbon isotopes suggest mainly C3 plant foods.
Megaladapis madagascariensis	−18.9, −22.4	*Megaladapis grandidieri, Lepilemur mustelinus, Avahi laniger, Megaladapis edwardsi, Alouatta Palliate*	Both SEM and low magnification microwear suggest consumption of leaves. This is consistent with the signal from dental morphology (the high shearing quotient).	Leaves. Stable carbon isotopes suggest mainly C3 plant foods.
Megaladapis edwardsi	−20.1, −20.2, −20.4			

(continued)

Table 1 (continued)

Taxon	$\delta^{13}C$ values	Primate species with most similar microwear profiles	Additional observations	Inferred diet
		Alouatta palliata, *Avahi laniger*, *Lepilemur leucopus*, *Megaladapis grandidieri*, *Megaladapis madagascariensis*, *Lepilemur mustelinus*	Both SEM and low magnification microwear suggest consumption of leaves. This is consistent with the signal from dental morphology (the high shearing quotient).	Leaves. Stable carbon isotopes suggest mainly C3 plant foods.
Archaeolemur majori	−18.3, −19.9, −20.5	*Archaeolemur edwardsi*, *Hadropithecus stenognathus*, *Cebus apella*, *Chiropotes satanas*, *Cacajao melanocephalus*, *Daubentonia madagascariensis*	Coprolites of a related species, *Archaeolemur* sp. cf. *edwardsi* from Anjohikely in the northwest, reveal the presence of bones of small animals (such as frogs) and shells of gastropods in addition to plant material.	Seed predator, hard object processor, omnivore. Stable carbon isotopes suggest mainly C3 plant foods.
Hadropithecus stenognathus	−8.4, −9.1, −13.22	*Archaeolemur majori*, *Archaeolemur edwardsi*, *Cebus apella*	Coarser microwear than in *Archaeolemur*. Both SEM and low magnification microwear studies suggest that *Hadropithecus* was not graminivorous, as had been previously thought.	Seed predator, hard object processor. Stable carbon isotopes suggest mixed C4 and CAM plants and/or animals consuming CAM and C4 plants. Likely omnivorous.

*Sources: Burney et al. (2004) for carbon isotopes; Godfrey et al. (2004) and Rafferty et al. (2002) for microwear. For additional information, see text.

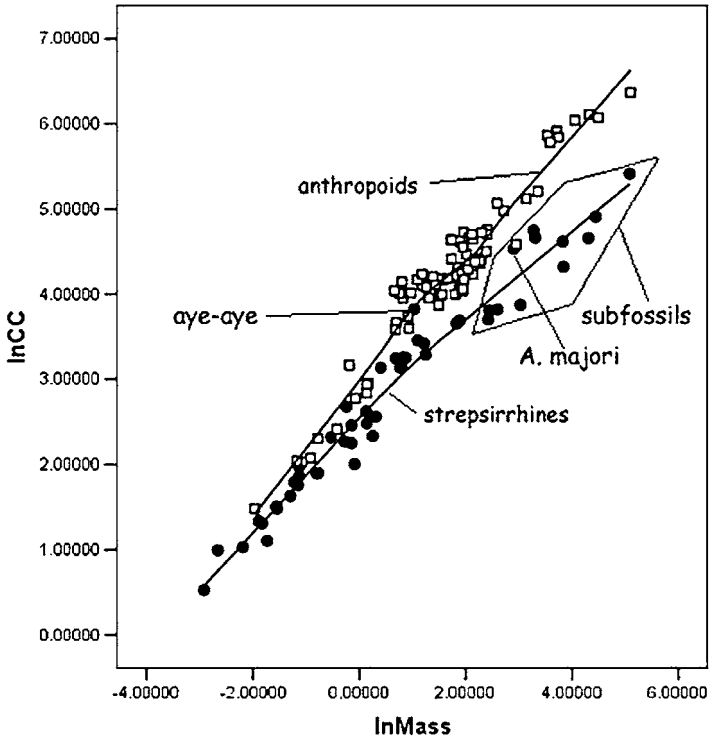

Fig. 2 Bivariate plot of logged cranial capacity (lnCC in ml) and logged body mass (lnMass in kg) in strepsirrhine primates (closed circles) and living anthropoids (open squares). The extinct giant lemurs are enclosed by a convex polygon, and nonparametric (LOESS) lines are fit to each group (tension = 0.7). Strepsirrhines fall consistently below size-matched anthropoids in brain size, although there are exceptions (e.g., the living aye–aye, *Daubentonia madagascariensis*, falls on the anthropoid line; *Archaeolemur majori* is virtually indistinguishable in its brain:body ratio from male proboscis monkeys (*Nasalis larvatus*)

Portraits of the Ghosts

We now present portraits of the extinct lemurs, focusing mainly on their trophic adaptations, as inferred from data on dental microwear, stable isotopes, and general morphology, as well as the pattern of growth and development, with special attention to age at M1 and M2 emergence, if known.

Palaeopropithecidae, or Sloth Lemurs

There are seven recognized species of sloth lemurs (Godfrey and Jungers, 2002), some apparently more folivorous than others, but all showing microwear

evidence of a mixed diet of foliage and fruit, and likely deliberate processing of seeds (Godfrey et al., 2004; Table 1). The seed-processing signal is strongest in *Babakotia radofilai* and *Mesopropithecus dolichobrachion*; *Mesopropithecus pithecoides* appears to have been more folivorous (Godfrey et al., 2004). In general, the sloth lemurs have microwear signals most similar to those of extant indriids and colobines. Their teeth resemble those of indriids, and their high shearing quotients suggest a similar ability to process leaves (Jungers et al., 2002).

Collagen-derived stable carbon isotopes ($\delta^{13}C$) range from -15.8 to -23.5, with less negative values in the arid south (*Mesopropithecus globiceps*) and more strongly negative values in the central highlands (*Archaeoindris fontoynontii*); see Burney et al. (2004). This range of $\delta^{13}C$ values suggests diets dominated mainly by C3 plant foods except in the more arid regions of Madagascar, where CAM plants were likely more important.

The sloth lemurs were poorly encephalized in comparison to size-matched anthropoids. The largest member of this clade, *Archaeoindris*, was similar in body size to male gorillas, but had a brain less than 40% of a gorilla brain in volume. The cranial capacity of *Palaeopropithecus ingens* barely exceeds 100 cc despite a body mass (~45 kg) in the bonobo-chimpanzee range; this is less than one-third the brain size of the African apes. The smaller sloth lemurs (*Babakotia* and *Mesopropithecus*) were similarly "small-brained." In terms of dental development, the palaeopropithecids were perhaps the most remarkable of the subfossils. Their rates of molar crown growth (measured here as the square root of the molar crown occlusal area divided by the crown formation time, or CFT, in days) are about six times as rapid as those of roughly like-sized

Table 2 Reconstructed body masses and average molar crown growth rates for extinct lemurs and like-sized anthropoid primates*

Taxon	Adult Female Body Mass (kg)	M1 Crown Growth Rate (mm^2/day)	M2 Crown Growth Rate (mm^2/day)
Palaeopropithecus ingens	41.5	0.071	0.063
Pongo pygmaeus	35.8	0.012	0.010
Megaladapis edwardsi	85.1	0.038	0.035
Gorilla gorilla	71.5	0.012	0.013
Archaeolemur majori	18.2	0.015	0.017
Papio hamadryas	11.4	0.017	0.019
Hadropithecus stenognathus	35.4	–	0.012
Pan troglodytes	33.7	0.010	0.008

*Crown growth rate = square root of molar occlusal area (md × bl in mm^2)/CFT in days. Dental measurements taken from unpublished data and from Swindler (2002).

anthropoids (such as adult female orang-utans; Table 2). Despite weighing over 40 kg as an adult (Jungers et al., 2008), *Palaeopropithecus ingens* would have had its first molar erupt only a few months after birth, just as in much smaller-bodied indriids, and earlier than in much smaller-bodied lemurids (Schwartz et al., 2002, Godfrey et al., 2006b); Table 3. Accelerated dental development is associated here with small adult brain size, early processing of solid food, and early acquisition of ecological independence.

Archaeolemuridae, or Monkey Lemurs

A very different developmental pattern characterizes the monkey lemurs (*Archaeolemur* spp. and *Hadropithecus*). These are the only giant lemurs whose molar CFTs approach those of like-sized anthropoids. In addition, encephalization is relatively high in the Archaeolemuridae. Indeed, *Archaeolemur majori* lies adjacent to the single anthropoid captured in the subfossil convex polygon seen in a plot of ln cranial capacity vs. ln mass (Fig. 2), *Nasalis larvatus* (males). *A. edwardsi* and *Hadropithecus stenognathus* are similar to *A. majori* in being the most encephalized subfossil lemurs, lying just to the right of *A. majori* and *Nasalis* on Fig. 2. In other words, the whole clade is relatively "big-brained" relative to other extinct lemurs. Among the living lemurs, only the aye–aye is similarly highly encephalized (Fig. 2; see also Bush and Allman, 2004; Kaufman et al., 2005).

Dental microstructural research on *Archaeolemur majori* and *Hadropithecus stenognathus* underscores developmental differences between the archaeolemurids and other giant lemurs (Godfrey et al., 2005, 2006b, c). The archaeolemurids are the only giant lemurs studied to date with molar crown growth rates roughly similar to those of like-sized anthropoids (Table 2). Furthermore, there is variation within the Archaeolemuridae: A hominoid-like dental developmental schedule characterizes only *Hadropithecus* (Table 3). Estimated crown formation time of an isolated M^2 of *Hadropithecus stenognathus* is 945 days (2.59 years) – twice as long as the reconstructed CFT for the second molar of *Archaeolemur majori*. Our samples of *Archaeolemur* and *Hadropithecus* studied to date suggest that the second molars did not begin to form until after birth, and that molar emergence occurred at a relatively advanced age – considerably later than in larger bodied subfossil species). We estimate M1 emergence in *A. majori* at around one and a half years, and M2 emergence by age 2 years (Table 3). In *Hadropithecus*, molar emergence was later yet. We only have a single molar (an M2) on which to base our dental chronology, but if we can assume a similar crown growth rate for both M1 and M2 (a reasonable assumption given the pattern observed in other subfossil lemurs; see Table 2), as well as a prenatal age for initiation of M1 formation similar to that of *Archaeolemur*, then we can estimate M1 CFT (987.5 days) and the age of M1 crown completion (902.5 days) in *Hadropithecus* on the basis of the size of the

Table 3 Life history inferences for extinct lemurs derived from dental microstructure, with comparative data for like-sized anthropoids*

Taxon	M1 CFT (days)	Age at M1 Crown Completion (days, years)	Age at M1 Emergence (years)	M2 CFT (days)	Age at M2 Crown Completion (days, years)	Age at M2 Emergence (years)
Palaeopropithecus ingens	221	34 days (0.09 yrs.)	~0.2–0.5	247	135 days (0.37 yrs.)	> 0.6
Pongo pygmaeus	993	969 days (2.66 yrs.)	~4.6	1267	(~5.0–5.5)	~5.0
Megaladapis edwardsi	380	248 days (0.68 yrs.)	~0.75–1.1	517	442 days (1.21 yrs.)	>1.4
Gorilla gorilla	1237	1212 days (3.32 yrs.)	3.3–3.5	~1250	(~5.0–6.0 yrs)	~6.6–6.8
Archaeolemur majori	522	437 days (1.20 yrs.)	~1.25–1.6	460	552 days (1.51 yrs.)	>1.7
Papio hamadryas	536	496 days (1.36 yrs.)	1.71	595	1095 days (3.00 yrs)	3.78–4.94
Hadropithecus stenognathus	–	–	–	945	~1037 days (2.84 yrs.)†	>3.0
Pan troglodytes	1004	968 days (2.65 yrs.)	2.7–4.1	1333	1820 days (4.99 yrs.)	5.3–8.3

*Sources: Schwartz et al. (2002, 2005), Godfrey et al. (2005, 2006b, c).

†Assuming a postnatal delay in the timing of initiation of M2 crown mineralization similar to that exhibited by *Archaeolemur*.

first molar. M1 was not crown-complete until almost 2.5 years after birth. This suggests an age for emergence (allowing for some root development) of the first molar not before 2.5 years and indeed probably closer to 3 years (approaching that of *Pan troglodytes*). Data for the second molar suggest an age of crown completion at around 2.8 years, and a likely age at M2 emergence between 3 and 3.5 years (Table 3).

There is strong evidence that all species of the genus *Archaeolemur* were generalists (i.e., mixed feeders consuming fruit with seeds, some foliage, and animal matter) as well as hard-object processors (Jungers et al., 2002; Godfrey et al., 2004, 2005; see Table 1). That evidence derives from the morphology of the teeth (Tattersall, 1973), the thickness and internal structure of the enamel (Godfrey et al., 2005), coprolites (Burney et al., 1997), and low magnification microwear (Godfrey et al., 2004, but see Rafferty et al., 2002) which resembles most closely that of *Cebus apella*, pitheciins, and, among lemurs, *Daubentonia* (Table 1). The molars of *Archaeolemur* are bilophodont, very like those of *Cebus apella* (King et al., 2005). The diet of *Cebus apella* includes, in addition to fruits and seeds (including palm nuts), insects, small vertebrates including titi monkeys (Sampaio and Ferrari, 2005), oysters (Fernandes, 1991), and crabs (Port-Carvalho et al., 2004; see also Rosenberger, 1992; Simmen and Sabatier, 1996). Nut-cracking is a skill acquired by infants through observational learning (Ottoni and Mannu, 2001). *Daubentonia madagascariensis* is also an extractive forager and omnivore with a diverse diet (Iwano and Iwakawa, 1988; Iwano et al., 1991; Sterling, 1994); delayed weaning allows youngsters to acquire a complex set of foraging skills, again through observation (Krakauer and van Schaik, 2005). Coprolites of *Archaeolemur* sp. cf. *edwardsi* reveal omnivory, with consumption of small vertebrates (frogs) and invertebrates (gastropods) as well as plants (Burney et al., 1997; Natalia Vasey and David Burney, Pers. comm.). Stable carbon isotope values ranging from −18.3 to −20.5 for *A. majori* in the south and west suggest mainly C3 plant consumption; more strongly negative values for *A. edwardsi* (−27.5) suggest C3 browsing perhaps in more densely wooded habitats, or on different plant species (Burney et al., 2004). Both species of *Archaeolemur* have stable carbon isotope values in the range of C3 plant consumers.

Like *Archaeolemur*, *Hadropithecus* shows evidence of hard-object processing and seed predation. Indeed the microwear signal (very heavy pitting and lots of scratches) bears testimony to an even coarser diet than in *Archaeolemur* (Rafferty et al., 2002; Godfrey et al., 2004, 2005), and it refutes the long-favored hypothesis that *Hadropithecus* was a specialized grazer and consumer of grass seeds (although it does not refute the possibility that grass was a component of its diet). Further evidence that the particular foods preferred by *Hadropithecus* were not the same as those preferred by *Archaeolemur* is provided by their very different stable carbon isotope values and dental morphology. Collagen-derived stable carbon isotopes of *Hadropithecus* range from −8.4 to −13.2 (Burney et al., 2004; Table 1), signaling primary consumption of C4 or CAM plants and/or animals consuming C4 or CAM plants. The morphology of the cheek teeth of *Hadropithecus* is distinctive, and

"designed" to produce a macrowear pattern that is unusual for primates. The posterior premolar and two anterior molars of *Hadropithecus* are disproportionately enlarged. When unworn, the molars exhibit a superficial bilophodonty, but the transverse crests remain sharp for a relatively short period. As they wear, dentine is exposed first at the tips of the cusps and then along the entirety of the crests. Each "crest" becomes a flat band or loop surrounding a dentine basin that soon coalesces with others to form a complex dentine lattice or network. These teeth are ideally shaped to trap objects (such as seeds) in the dentine basins, holding them in place while they are subjected to high crushing and grinding forces. Overall, the macrowear pattern is reminiscent of those of certain ungulates. The cranial architecture (especially the mandibular corpus) is extremely robust, as might be expected of a seed predator or hard-object processor (Godfrey et al., 2005; Norconk et al., 2006). Burney et al. (2004) and Godfrey et al. (2005) suggested that consumption of terrestrial snails (that in turn consumed C4 or CAM plants) may have contributed to the weakly negative stable carbon isotope signal exhibited by *Hadropithecus*. *Paranthropus* was suggested as a trophic analogue (Godfrey et al., 2005); it is noteworthy that *Paranthropus* was a likely omnivore and hard-object processor, athough its stable carbon isotope values signal a higher percentage of C3 foods in its diet (see, for example, Lee-Thorp et al., 1994, 2000; Peters and Vogel, 2005). Other possible analogues may be peccaries (Tayassuidae) – omnivores that feed selectively on CAM plants (including the hard seeds of Euphorbiaceae; Ilse and Hellgren, 1995; Benirschke et al., 1990), have a similar macrowear pattern, and similar microwear pattern (Semprebon, unpubl. data). Peccary stable carbon isotope signatures (MacFadden and Cerling, 1996) are somewhat different from those of *Hadropithecus*, which may simply reflect different combinations of foods with CAM or C4 metabolism. Peccaries and suids are also among the many omnivorous mammals that have been reported to consume land snails (Benirschke et al., 1990; Allen, 2004). Peccaries are frugivore/herbivores, eating mainly fruits and other fleshy plant parts. They are both seed predators and dispersers.

Among extant primate species, extractive foragers and hard-object processors tend to have the most protracted life histories and the largest brains. Gibson (1986) related exceptionally high encephalization (within respective clades) to omnivory and extractive foraging in *Homo*, *Pan*, *Cebus* and *Daubentonia* (see also Parker and Gibson, 1977). The archaeolemurids contrast strikingly with the palaeopropithecids in exhibiting much higher encephalization and much slower dental development, as well as a much coarser dietary signal. Slow dental development may signal delayed weaning and a prolonged period of infant and juvenile dependency, during which time the foraging skills associated with a diverse diet and hard object processing must have been acquired (much as in *Cebus apella* or *Daubentonia madagascariensis*) (Fragaszy et al., 1991; Fragaszy and Adams-Curtis, 1997; Krakauer and van Schaik, 2005).

Megaladapidae, or Koala Lemurs

Although the three recognized species of *Megaladapis* vary considerably in estimated body size (from ~45 to 85 kg), they share a similar and unique Bauplan. They were specialized arboreal folivores with some morphological convergences on *Phascolarctos*, the Australian koala (Tattersall, 1972; Walker 1974; Jungers, 1978). In terms of dental development and life history strategies, they appear to have been more like the large-bodied sloth lemurs than the monkey lemurs (Schwartz et al., 2005; 2007; Godfrey et al., 2006b) (Tables 2 and 3). Body proportions and their huge grasping hands and feet (Wunderlich et al., 1996; Jungers et al., 2002) suggest that they were slow-moving climbers at home in the trees.

They share with *Lepilemur*, convergently it would appear (Karanth et al., 2005), a suite of craniodental adaptations linked to a predominately leaf-eating diet (e.g., loss of upper central incisors as adults and "cresty" molars with marked ectolophs). Both SEM and reflected light microscopy microwear analyses of the molars reveal a predominance of scratches and very few pits (Rafferty et al., 2002; Godfrey et al., 2004), a pattern characteristic of dedicated browsers (e.g., howler monkeys, *Avahi,* sportive lemurs). Data on stable isotopes also corroborate the reconstruction of forest browsing in megaladapids; C3 plant consumption is consistent with $\delta^{13}C$ values ranging from −18.9 to −22.4 (Table 1). As primary folivores, it seems highly unlikely that the koala lemurs were major players in seed dispersal.

Compared to like-sized anthropoids (e.g., orang-utans, chimpanzees and female gorillas), all three species had relatively very small brains. Whereas the endocranial volumes of female gorillas average around 460 cc, the cranial capacity of the similarly sized *M. edwardsi* is only ~30% of this value (also see Radinsky, 1970). Permanent teeth erupted quite early and weaning probably also occurred relatively early in koala lemurs (although not as precociously as in sloth lemurs), and there is little to suggest a prolonged period of infant learning prior to their becoming "ecological adults" (Schwartz et al., 2005; Godfrey et al., 2006b).

Other Ghosts

Daubentonia robusta appears to have been a much larger, more robust version of its congener, the living aye–aye (Grandidier, 1929). It shares the highly derived complex of skeletal features linked in *D. madagascariensis* to extractive foraging on structurally-defended resources (Sterling, 1994), including chisel-like, continually-growing incisors and an elongate, filiform third digit of the hand (Lamberton, 1934*)*. Living aye-ayes are seed predators par excellence, supplementing a diet of nuts and fruits with insects and larvae. In view of its much larger body mass (ca. 15 kg), it is likely that *Daubentonia robusta* relied

even more on seeds than its congener. Limited stable carbon isotope data (one $\delta^{13}C$ value of −16.3; Burney et al., 2004) suggest predominantly C3 foraging. Although the postcranial skeleton is well known (Simons, 1994) – and points to a deliberate, arboreal quadruped with relatively short and robust limbs (Jungers et al., 2002) – there are no known crania or cheek teeth. On the basis of its remarkable similarity to the highly encephalized living aye–aye and a comparable adaptation to extractive foraging, we suspect that its cranial capacity was also relatively large. Food-hoarding or caching behavior may or may not have characterized *D. robusta*; it has been observed in *D. madagascariensis* in captivity (Iwano, 1991) but not in the wild (E. Sterling, pers. commun.). Nuts are sometimes retrieved from epiphytes or the ground, but generally where they could have fallen.

Although roughly three times its body size, *Pachylemur* is clearly the sister taxon of *Varecia* (Szalay and Delson, 1979; Crovella et al., 1994). The two recognized species of *Pachylemur* (*insignis* and *jullyi*) are similar in morphology and body size, but can be distinguished reliably by both geography and details of the dentition (Vasey et al., 2005). Dental anatomy and microwear are consistent with a predominantly frugivorous diet, similar to those of frugivorous lemurs (Table 1; Seligsohn and Szalay, 1974; Godfrey et al., 2004). The macrowear pattern and presence of caries further corroborate this reconstruction (Vasey et al., 2005). Relatively low pit counts suggest that *Pachylemur*, like other lemurids, tended to spit seeds or swallow them whole; it is therefore an excellent candidate for being an agent of seed-dispersal in the recent past. Available stable isotope data are compatible with C3 foraging ($\delta^{13}C$ values of −20.0 to −20.2). As is characteristic of most extinct lemurs, the limb bones of *Pachylemur* are relatively short and robust, and the overall form of the postcranium implies arboreal quadrupedalism (with little evidence for leaping but some suspension as in *Varecia*). With a cranial capacity of ∼45 cc, both species had brains roughly half (or less) of body-size matched anthropoids (e.g., some macaques and odd-nosed colobines). Although much remains to be done on the dental and somatic development of this genus, preliminary data suggest a developmental pattern similar to those manifested in *Varecia* and other lemurids.

Madagascar: Past and Present

Our task in this section is to place the ghosts into their paleoenvironmental contexts, and to review what is known about changes in those environments from the past to the present. We ask: What is unique about Madagascar's ecosystems? What has changed since the arrival of humans? Do the plant communities of Madagascar today have anachronistic species? Our discussion is intended not to be exhaustive but rather suggestive. Clearly much more

research is required to elucidate details, and to identify additional plant groups of interest.

What's Special about Madagascar's Ecosystems?

It is common knowledge that the lemurs of Madagascar display a unique suite of behavioral and physiological characteristics (see reviews by Wright, 1999; Gould and Sauther, 2006). These have been understood not merely as accidents of history but as adaptations to the unusual structure and low productivity of Madagascar's forests, in turn affected by Madagascar's unpredictable climate and nutrient-poor soils (Ganzhorn, 1995; Reed and Fleagle, 1995; Fleagle and Reed, 1996; Goodman and Ganzhorn, 1997; Wright, 1999; Grubb, 2003; Reed and Bidner, 2004; Gould and Sauther, 2006). The peak fruit production season in Malagasy rain forests is approximately three months shorter than in rain forests in the Amazon or continental Africa (Wright et al., 2005). Certain plant groups, such as figs (Moraceae), are poorly represented on Madagascar; elsewhere, they are important keystone species for many animal groups, including primates (Terborgh, 1986a, b; Shanahan et al., 2001). Goodman and Ganzhorn (1997) have posited that the rarity of figs contributes to the relatively low number of primate frugivores on the island.

Yet, in some ways, the habitats of Madagascar are quite suitable for nonhuman primates – at least they were so until the arrival of humans. An extraordinary number of primate species, ranging in body size from 30 g to 160 kg, evolved on an island less than 600,000 km^2 in area, and primates comprise one of the dominant elements of Madagascar's mammalian fauna. There are 16 recognized extinct lemur species (and an additional one in the process of being described) and more than 50 extant ones. More than 20 primate species may have coexisted in single forests prior to the megafaunal extinctions of the Holocene (Godfrey et al., 1997b). Despite the dearth of figs species on the great red island, other plants that are favorite resources for primates are well-represented. Madagascar has many tree species with dull-colored, fiber-rich fruits that appeal to lemurs or other mammals with poor color vision. This contrasts sharply with other regions (such as South Africa) sporting many more sugar-rich, "bird-colored" fruits appealing to frugivorous birds with excellent color vision (Dominy et al., 2003; Voigt et al., 2004). A number of Madagascar's plant families have representatives elsewhere in the world that are well-exploited by primates, not merely for their leafy vegetation, but for their edible fruits and/or seeds. Even regions receiving very low annual rainfall (southern and southwestern Madagascar) are able to support many species of primates, due to unusually high humidity, which promotes the establishment of thicket rather than open savanna (Grubb, 2003). The thickets of the south are the so-called spiny forests, dominated by succulents. Gallery forests with a wide range of deciduous plant species line the rivers of the southwest, some of which are dry

for all but a few months out of the year. The south is today inhabited by primates belonging to the families Indriidae, Lepilemuridae, Lemuridae and Cheirogaleidae (often at higher densities than in the eastern forests; Irwin, 2006b), and in the past also by members of the Megaladapidae, Daubentoniidae, Archaeolemuridae, and Palaeopropithecidae.

As might be expected given its long geographic isolation, Madagascar harbors a unique biota (i.e., with some taxa absent or poorly represented and others unusually speciose) and virtually unparalleled levels of endemism, both regionally and island-wide. The biotic diversity of Madagascar was recently reviewed by Goodman and Benstead (2005) on the basis of contributions to their edited volume, *The Natural History of Madagascar* (Goodman and Benstead, 2003). Levels of endemism are high for all groups of Malagasy vertebrates (for example, 100% of the total of 101 species of non-volant mammals, 99% of 199 species of frogs, over 90% of about 340 reptiles, and over 50% of more than 200 species of birds; Goodman and Benstead, 2005). Some invertebrate groups have equally high endemism; for example, terrestrial gastropods, with 671 species, have 100% endemicity (Goodman and Benstead, 2005). Mollusc and crustacean species are poorly known (Goodman and Benstead, 2005), but they number in the thousands, and do exhibit regional endemism.

Levels of endemism are also exceptional for major groups of plants. Euphorbiaceae, with 700 species, is the most speciose terrestrial plant family on the island; most are endemic (Hoffmann and McPherson, 2003; Goodman and Benstead, 2005). Along with the Didiereaceae, euphorbs are the dominant flora of the arid south. Other plants common in the spiny forests include the families Crassulaceae (*Kalanchoe* spp.) and Cucurbitaceae. All four use CAM photosynthetic pathways (Winter, 1979).

The Rubiaceae, or coffee family, is the second most speciose family of terrestrial plants on Madagascar, with more than 650 species and 98% endemicity (Davis and Bridson, 2003). Also extremely speciose on Madagascar is the Fabaceae (legumes), with 573 species and 80% endemicity (Du Puy et al., 2002; Labat and Moat, 2003; Goodman and Benstead, 2005), including the subfamilies Papilionoideae and Mimosoideae.

Palms (Arecaceae, including 170 species with 98% endemicity) are the 4th most speciose family of Malagasy terrestrial (non-marine) plants, excluding ferns and fresh-water aquatic plants (Goodman and Benstead, 2005). Palms are common in arid regions of Madagascar (including the palm savannas of the north and northwest), but also in the lowland rain forests of the east. Palms are also found in the highland rain forests.

The Pandanaceae (pandans, or screw pines) are another dominant floral component of the lowland rain forests, and are particularly common along rivers and streams. There are 99 pandan species in Madagascar, and 100% are endemic (Goodman and Benstead, 2005). Also speciose in Madagascar is the Clusiaceae (a large pantropical family including *Calophyllum* and *Garcinia*, two favorites of many lemur species; Birkinshaw and Colquhoun, 2003).

Other plant groups are less speciose, but are nevertheless important elements of the flora of Madagascar. They include the bamboos (Poaceae: Bambusoideae), the baobabs (Malvaceae), and the Strelitziaceae (Madagascar's "Traveller's tree" and its relatives). There are 34 species of bamboos on Madagascar; all are endemic (Goodman and Benstead, 2005). Only seven species of baobabs exist on Madagascar, but these too are mostly endemic (Goodman and Benstead, 2005).

Most of the speciose terrestrial plant groups are important resources for living lemurs (Birkinshaw and Colquhoun, 2003) and most were probably eaten by the extinct lemurs as well. The plants most exploited (and dispersed) by living lemurs belong to the families Euphorbiaceae, Fabaceae, Rubiaceae, Clusiaceae and Moraceae (Birkinshaw, 2001; Birkinshaw and Colquhoun, 2003). Of these, only the Moraceae (figs) is not speciose in Madagascar; however, figs are selectively favored by many lemurids and may, for them, serve as keystone species, providing food during times of otherwise scarce resources. Bamboos (Poaceae) comprise the primary, year-round, foods for one clade of living lemurs (*Hapalemur* spp.), but are more rarely consumed by others, if at all. Other groups that are not speciose in Madagascar, but are sought out by some lemur species, include the Sapindaceae and the Combretaceae.

Some parasitic plants (mistletoe, genus *Bakerella*, family Loranthaceae) are important keystone resources for both small- and larger-bodied extant lemurs (see Atsalis, 1999, on *Microcebus rufus*; Irwin, 2006a, on *Propithecus diadema*). Arecoid palms with relatively small seeds (e.g., *Dypsis decaryi*) are dispersed by lemurids (Ratsirarson and Silander, 1997; Overdorff and Strait, 1998; Birkinshaw, 2001; Ratsirarson, 2003) and other vertebrates; palms of various sizes are keystone species for primates outside Madagascar (Terborgh, 1986a, b; Dominy et al., 2003).

Along with figs (Moraceae), the Euphorbiaceae, Papilionoideae, Mimosoideae, and Sapindaceae are among the plant groups that are universally exploited by primate seed predators across the Neotropics, continental Africa, and Asia (Norconk et al., 2006), and it is likely that they were eaten by the extinct seed predators of Madagascar as well. Living-lemur seed predators do in fact exploit these families; for example, seeds of palms (Arecaeae) are consumed by *Daubentonia madagascariensis*, and seeds of euphorbs as well as many other plant families are eaten by sifakas. Other families favored by aye-ayes include the Burseraceae (ramy) and the Combretaceae; these families are also exploited by other living lemurs.

Baobabs have a wide range of dispersal mechanisms. On continental Africa, some are dispersed by baboons and other mammals (Peters, 1993). Some pandan fruits are eaten and the seeds dispersed by living lemurids (Birkinshaw, 2001; Callmander and Laivao, 2003). Lemurids also exploit the nectar of the Traveller's tree (Strelitziaceae); in doing so, they become important pollinators (Kress et al., 1994; Birkinshaw and Colquhoun, 2003). Seeds of the Traveller's tree have been reported only in the feces of the largest-bodied living lemurid, *Varecia* (Dew and Wright, 1998).

What's Changed since the Arrival of Humans?

In the past 2000 years, Madagascar lost its "megafauna" – its giant lemurs, pygmy hippopotamuses, giant tortoises and crocodiles, and flightless elephant birds. Many other native or endemic species disappeared, generally the largest-bodied members of their respective orders or families on Madagascar, including rodents, carnivores, bats, fishes, and flighted birds. Humans introduced animals from southeast Asia and Africa, including horses, cattle, bush pigs (*Potamochoerus larvatus*), domestic pigs (*Sus scrofa*), goats, sheep, dogs, cats, poultry, *Viverricula indica* (small Indian civet), and, of course, rats and mice.

Figure 3 provides a summary of the trophic changes in Malagasy primates that have occurred over the past two thousand years (Godfrey and Irwin, in press). Of a total of 64 species analyzed, 17 are extinct and 47 extant.[1] Each species is classified as belonging to one of five guilds according to the observed or reconstructed major components of their diets: hard-object processors/seed predators; mixed feeders/seed predators; specialized folivores; medium to large-bodied frugivores (dispersers of seeds of various sizes, including some large ones); and small-bodied insect, fruit, and/or gum consumers (potential dispersers of small seeds).

(1) Almost 30% of the primate species that became extinct were hard-object processors; they comprised almost 10% of the primates living on Madagascar in the past. Included in this guild are all of the Archaeolemuridae and the Daubentoniidae, along with one palaeopropithecid – *Babakotia radofilai* (identified by Rafferty et al., 2002, as a hard-object processor, and by Godfrey et al., 2004, as a *Pithecia*-like seed predator, with the coarsest diet of all palaeopropithecids). The sole living member of this guild is *Daubentonia madagascariensis*.

(2) Approximately 35% of the primate species that became extinct were mixed feeders on foliage and fruit, and likely seed predators. This guild, including most of the Indriidae, is moderately well represented in Madagascar today (8.5% of Madagascar's extant primates), but was much better represented in the past (with over 15% of the primate species living in the recent past). Living members of this guild are physiological folivores and efficient predators on seeds. Most of the Palaeopropithecidae (the most speciose of the families of extinct lemurs) are included in this guild.

(3) The percentage of Madagascar's primate species that can be considered specialized folivores has remained roughly constant from the past to the present, at almost 30%. This guild includes all of the Lepilemuridae and Megaladapidae, and the most folivorous indriids (*Avahi* spp.),

[1] The taxonomy of extant lemurs is under revision as new species, particularly of cheirogaleids, are being discovered and named. For a complete list of species analyzed, see Godfrey and Irwin (in press).

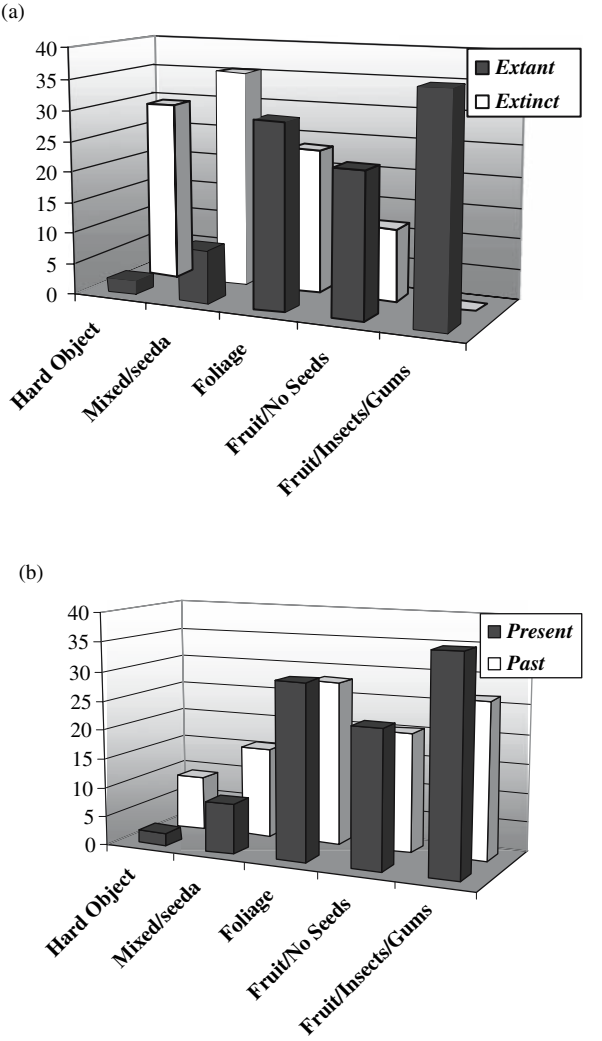

Fig. 3 Relative percentages of lemur species in each of five trophic guilds. (a) Extinct vs. extant lemurs. (b) Species living in the recent past (i.e., extinct plus extant) vs. those still extant. Data from Godfrey and Irwin (in press)

palaeopropithecids (*Mesopropithecus pithecoides*), and lemurids (the bamboo lemurs, *Hapalemur* spp.). Foliage consumption in the past was as high among lemurs as it is in the present.

(4) Living and extinct lemurids (with the exception of the bamboo lemurs) are classified here as mixed feeders with a preference for fruit. In consuming ripe fruit without chewing the seeds, living members of this guild disperse small, medium, and large seeds, thus the label "Fruit/No seeds." Approximately 20% of the primate species in the past and the present belonged to this guild. The percentage has changed trivially with the extinction of *Pachylemur* spp. This guild is relatively small today, as it was in the past.

(5) All of the Cheirogaleidae are classified here as members of a guild consuming fruit, insects, and gums. Some are more frugivorous, others are more insectivorous, and still others are gum specialists. Leaves are a rather trivial component of their diets. The relative percentage of cheirogaleids has increased from the past to the present by virtue of the loss of species belonging to other trophic guilds (there are no known extinct cheirogaleids). They now comprise more than 35% of living lemurs. The more frugivorous cheirogaleids are important dispersers of plants with small fruits and seeds, but they are not effective large-seed dispersers. Food selection by potential seed dispersers is correlated with fruit size and seed size (Bollen et al., 2004a, b); today on Madagascar, larger-bodied frugivores (such as *Eulemur* spp.) disperse larger-seeded plant species, while bats, frugivorous birds, and cheirogaleids disperse smaller-seeded plants (Bollen et al., 2004a).

Ecological Anachronisms, or Plants without Partners?

The orphans of the plant world have a number of identifying characteristics (Barlow, 2000; Chapman and Chapman, 2002). First, they must be native to the affected forests. Secondly, they have physical adaptations for, or geographic distributions indicative of, zoochory, but no obvious extant seed dispersers. Their fruits may be underexploited (e.g., rotting in large numbers under their parent trees). If sufficiently impacted, orphaned species may have limited (non-viable) geographic distributions. Their primary dispersal agents may be recently-introduced (non-endemic) animals. Many plants that were dispersed by megafauna have unusually large seeds.

It is usually easy to tell whether fruits are adapted for mechanical, wind, water, or animal dispersal. Those that depend on endozoochory (dispersal after passage through an animal's gut) have mechanisms to attract a particular set of dispersers (e.g., special colors or odors), even if they do not rely on a single, co-evolved partnership. Generally, there will be a nutritious, edible pulp (it may be rich in lipids or sugar, again, depending on the intended consumer); the seeds themselves may be hard or protected by a thick testa to survive transport through a gut. The pericarp may be brittle or easy to crack open when the seeds are mature and ready for ingestion. Often, the fruits will be "indehiscent" (they will not open to release their seeds). The seeds will show no adaptations for wind (e.g., wings or parachutes) or water (e.g., buoyancy) dispersal; the plants themselves may occur far from waterways.

We know of no comprehensive review of possible Malagasy plant anomalies, but the question has certainly been raised in the literature with regard to particular plant groups. Dransfield and Bentje (1995a, b), for example, discuss apparently orphaned palms – species that (1) are found at a distance from water, (2) appear to require zoochory but have no known seed disperser other than introduced species, such as bush pigs, (3) survive far from rivers or streams

only by virtue of their resistance to fire, or (4) have very restricted geographic distributions (e.g., *Ravenea*, the single palm of the spiny forest). The dull color of palm fruits suggests predominant mammal dispersal. The large size of the seeds of some species suggests prior dispersal by primate or other megafauna.

Living lemurids are known to disperse seeds as large as 10–20 mm (or even more – up to 40 mm) in at least one dimension (Ganzhorn et al., 1999; Birkinshaw, 2001). These include *Strychnos decussata* (Loganiaceae), *Cordyla madagascariensis* (Fabaceae), *Capurodendron rubrocostatus* (Sapotaceae), *Sorindeia madagascariensis* (Anacardiaceae), *Canarium madagascariense* (Burseraceae), *Terminalia* spp. (Combretaceae), *Plagioscyphus* sp. (Sapindaceae), *Macphersonia madagascariensis* (Sapindaceae), and *Chrysophyllum perrieri* (Sapindaceae).

There are, however, living on Madagascar today, some plants with fruits and seeds too large to be dispersed by any extant Malagasy animal. One such tree with no known seed disperser is *Dilobeia* (Proteaceae) (Turk, 1997). This eastern rain forest tree produces single-seeded fruits with seeds 3–4 cm by 2–2.5 cm. Other examples include the borassoid palm genera *Borassus*, *Hyphaene*, *Bismarckia* and *Satranala*, and the arecoid palms *Orania* and *Lemurophoenix* (Dransfield and Bentje, 1995b). Elsewhere in the Paleotropics, relatives of *Borassus* are dispersed by orang-utans, bats, elephants, and baboons (Zona and Henderson, 1989). In the Neotropics today, large-seeded palms are dispersed by capuchin monkeys, peccaries (Tayassuidae), and tapirs (Tapiridae) (Terborgh 1986a, b; Zona and Henderson, 1989; Fragoso, 1997; Fragoso and Huffman, 2000; Quiroga-Castro and Roldán, 2001).

Some Malagasy baobabs (genus *Adansonia*, Malvaceae) are likely orphans (Baum, 1995, 2003). *Adansonia grandidieri* and *A. suarezensis* in particular have fruit with fragile pericarps and tasty, nutritious pulp, and their seeds are protected by tough, thick testa. These species have restricted geographic distributions today. Whereas they are clearly adapted for animal dispersal, no extant animal disperser is known, and Baum (1995, 2003) suggests that the seeds of *Adansonia grandidieri* and *A. suarezensis* may have been dispersed by extinct lemurs (possibly *Archaeolemur*). *Adansonia* seeds on continental Africa are mammal-dispersed (elephants, baboons; Peters, 1993; Baum, 1995).

Ramy nuts (*Canarium madagascariense*, Burseraceae) are a favorite resource for aye-ayes (Iwano and Iwakawa, 1988). The whole fruits are about 60–70 mm long and 40–50 mm wide, and have substantial flesh. Each has a single seed about 40 mm long and 20 mm wide. These seeds are eaten by aye-ayes, who remove just enough flesh to expose the top of the seed and carve into it using their incisors. It is likely that a fruit with this much flesh evolved to attract a large-bodied seed disperser, and that the predatory aye–aye is in essence an intruder on the system. The only frugivorous lemur large enough to swallow these seeds intact today is *Varecia variegata* (Dew and Wright, 1998). Relatives of the Malagasy *Canarium* species in Thailand are dispersed by very large birds (hornbills and one large parrot; see Kitamura et al., 2006); large birds or mammals (most likely, including *Pachylemur*) certainly did the same in Madagascar.

Other Malagasy plants may be underexploited by animals today, but may well have served Madagascar's megafauna. Little is known about the reproductive biology of Malagasy pandans. Lemurs do sometimes disperse their seeds (Callmander and Laivao, 2003), although species common near waterways are also dispersed by water. The seeds themselves are nutritious but well adapted for animal dispersal, as they are well protected by a hard endocarp, and difficult to cut even with a knife (Callmander, pers. commun.). Most Malagasy pandan seeds do not exceed 20 mm in width, but the largest are 30–40 mm wide (Callmander, pers. comm.). However, even the largest Malagasy pandan seeds easily could have been swallowed whole and dispersed by frugivores only slightly larger than the largest living lemurids. Given their hardness, pandan seeds would have been vulnerable to predation only by skilled extractive foragers.

Madagascar's flagship tree is the "Traveller's tree," *Ravenala madagascariensis*, (Strelitziaceae); it thrives in monocultures in degraded forests of eastern Madagascar largely by virtue of its vegetative reproduction. The seeds are moderately large (generally over 10 mm) and are not adapted for wind or water dispersal (Calley et al., 1993). *Ravenala* produces a "fan" with brown bracts and hard seeds surrounded by odoriferous light blue integuments or arils. Similarly-adapted plants provide nourishment in the aril; the seeds are adapted to pass through the gut unharmed (Calley et al., 1993). However, Dew and Wright (1998) have found viable seeds of *Ravenala* only in the dung of the largest-bodied living lemurid, *Varecia variegata*. The primary disperser for the Traveller's tree may have been the larger-bodied *Pachylemur*. How such a plant might fare following extinction (or local extirpation) of its endemic seed dispersers is difficult to predict, given its obvious success at colonizing areas that have been denuded by humans. Aggressive vegetative reproduction can create huge stands, albeit lacking in genetic diversity. Ultimately, however, without dispersal partners, the fate of the Traveller's tree may parallel that of the "double coconut" or "coco-de-mer" (*Lodoicea maldivica*) – a borassoid palm today endemic to two small islands in the Seychelles, where it is highly endangered but well represented in a few lingering stands. With fruit weighing in excess of 20 kg and bearing the largest known seed (Edwards et al., 2002), this species has apparently survived long after the demise of its natural dispersers (Corner, 1966). Mabberley (1983, 1988) considers it the earth's most spectacular dispersal anachronism. Unlike the coconut, viable fruit of the double coconut do not float and the seeds are killed by sea water.

Primate Portraits in Ecological Perspective

We now come full circle to the question posed at the start: Can we use our knowledge of life history and trophic characteristics of giant lemurs to identify likely partners for Madagascar's orphaned plants? Which primate niches, if any, have been vacated during the recent extinctions?

Birkinshaw (2001: 484, following Richard and Dewar, 1991) suggests that the extinct lemurs *Pachylemur* spp. and *Archaeolemur* spp. probably belonged to the large-seed dispersal guild. To this we add *Hadropithecus stenognathus*, with the caveat that *Archaeolemur* and *Hadropithecus* were probably primarily seed predators and occasional seed dispersers, while *Pachylemur* was undoubtedly primarily a seed disperser and occasional seed predator. Ecologically, these primates served critical roles in the wooded ecosystems of Madagascar, much like the capuchins, peccaries, atelines, tapirs (and formerly, the gomphotheres, ground sloths, and equids) of the Neotropics, as well as the cercopithecines, apes, and elephants of the Paleotropics. We believe that the palaeopropithecids and megaladapids would have played a lesser role. The former were probably more like colobines and indriids (i.e., mixed feeders and sometimes deliberate seed predators, but very destructive to seeds); the latter were more strictly folivorous. *Daubentonia robusta* would have been, like its congener, a seed predator par excellence, and probably a seed disperser only if it was also a hoarder.

We recognize that seed dispersal is commonly achieved through diverse, essentially redundant, systems (Chapman and Chapman, 2002; Bollen et al., 2004a, b); plant species rarely depend on single co-evolved dispersal partners (Bodmer, 1991; Garber and Lambert, 1998). Certainly on Madagascar, non-primates, including large-bodied reptiles and elephant birds, as well as the omnivorous carnivores endemic to the island, would have contributed to large-seed dispersal. Lord et al. (2002) make a convincing case that moas were important seed dispersers in New Zealand. Collagen-derived stable carbon isotopes of elephant bird bone range from −13.25 to −24.9 (Burney et al., 2004), suggesting strong dietary diversity, and, at the less negative end of the range, a mixed diet including C4 or CAM plants. Dransfield and Bentje (1995a) suggest that *Satranala* may have been dispersed by elephant birds. But primates process seeds differently than birds, and some large-seeded plants may depend on large-bodied frugivores to swallow and defecate seeds; they may not do as well when seeds are spit or regurgitated (Dominy and Duncan, 2005). Endozoochory contributes to long-distance seed dispersal as seed spitting cannot; according to the Janzen-Connell hypothesis (see Ganzhorn et al., 1999), seeds dropped near parent plants are unlikely to be successful. Ingestion can enhance seed germination by several means (Rick and Bowman, 1961; Traveset and Verdú, 2002; Robertson et al., 2006): 1) scarification (slight damage to seed coats increases permeability to water and gases); 2) deinhibition (some seeds will not germinate without pulp removal, because pulp can function as an inhibitor of germination); and 3) fertilization (faecal material nourishes seeds, and can therefore trigger germination).

Pachylemur was undoubtedly the most effective large-seed disperser in the Order Primates on Madagascar. It was the largest-bodied member of a family of effective dispersers of medium or large seeds; lemurids tend to swallow seeds whole or with minimal damage, and seeds passing through their guts have demonstrated high germination success (Dew and Wright, 1998; Birkinshaw, 2001). In the eastern rain forest, fruits with large seeds (>10 mm in length) are

dull-colored (green, brown, tan, purplish, or black) and primate-dispersed, while fruits with seeds smaller than 10 mm are generally red, yellow, orange, pink, blue, or white and not primate-dispersed (Dew and Wright, 1998, on *Eulemur rubriventer*, *Eulemur fulvus*, and *Varecia variegata*). The same pattern holds for *Eulemur macaco* in the northwest (Birkinshaw, 2001), and *Eulemur collaris* in the southeast (Bollen et al, 2004a, b). In the dry forest in western Madagascar today, only the introduced bush pig *Potamochoerus larvatus* and endemic *Eulemur fulvus rufus* (the largest-bodied lemurid remaining in the west) ingest seeds larger than 11 mm in length (Ganzhorn et al., 1999). Species belonging to the genus *Pachylemur* were widespread in Madagascar, from the southern to the northern tips of Madagascar and into the central highlands (Godfrey and Jungers, 2002). They occupied sites with extant lemur communities much like those of modern eastern rainforests (Godfrey et al., 1999); this suggests that *Pachylemur* also occupied at least some eastern rain forests (where there are no subfossil sites). Thus, most, if not all, of Madagascar's forests would have had large and smaller-bodied lemurids acting as their primary seed dispersers. We know that *Varecia* can swallow seeds intact with diameters of over 30 mm (Dew and Wright, 1998) and that *Eulemur* can do the same for seeds with diameters of 20–30 mm (Birkinshaw, 2001). If the ratio of seed width to the cube root of body mass were similar for *Pachylemur* and *Eulemur*, then *Pachylemur* would have been able to swallow seeds with diameters up to ~50 mm – perhaps more.

It is likely that Madagascar's primate seed predators also played an essential role in seed dispersal. We hypothesize that this was the case for the Archaeolemuridae, who were considerably larger in body size than the largest species of *Pachylemur* and had much more robust jaws. Seed predators may contribute to the process of seed dispersal in a number of ways (Norconk et al., 1998). First, and importantly, they may regularly open fruits that are difficult for species with less robust jaws to process, making available to other species (including benign frugivores) discarded fruit pulp with untouched seeds. Elsewhere in the world, palm nut exocarp and mesocarp are eaten by many species (including very small-bodied species), but the fruits must be opened by animals with jaws powerful enough to do so, or the ability to use tools to crack them open (Boesch and Boesch, 1983; Visalberghi, 1990; Anderson, 1990; Daegling, 1992; Anapol and Lee, 1994; Inoue-Nakamura and Matsuzawa, 1997; Ottoni and Mannu, 2001; Fragaszy et al., 2004; Wright, 2005). Secondly, seed predators disperse seeds by passing through their guts the occasional seed that is minimally injured (or not at all). Germination success of intact seeds varies by species, and may depend on internal digestive processing, including gut transit time. Among living species, the ability to function as an effective seed disperser seems to be inversely correlated with transit time; thus, for example, the most effective seed dispersers among primates (e.g., the more frugivorous atelines and lemurids) have short transit times, whereas species with longer gut transit time (such as indriids) tend to be less effective. Thirdly, if seed predators hoard fruits or seeds (in the manner of rodents), then seeds in forgotten caches will have been inadvertently dispersed.

Faunivores tend to have fast transit times, followed by omnivores and frugivores; folivores have slow transit times (Lambert, 1998). Diet is more important than body size in determining transit time (Lambert, 1998). This is because, to ensure effective nutrient processing, foods (such as fruit) that are high in soluble carbohydrates must pass through the gut more quickly than foods (such as leaves) that require long fermentation for effective nutrient uptake (Milton, 1984; Lambert, 1998). Indeed, Milton (1986) described an efficiency-velocity tradeoff in primates and other animals: species that maximize nutrient extraction and thus gut efficiency (folivores, with long gut retention) necessarily compromise their capacity to exploit fruit regularly, whereas frugivores, with short gut transit time can maximize the total mass of food processed per unit time at the expense of being able to process leaves effectively. The combination of digestive anatomy (the length and complexity of components of the digestive tract) and transit time constrains diet; frugivores actually require fast transit, while folivores require prolonged fermentation and slower transit (Milton, 1993; Lambert, 1998). Among extant lemurs, the relevant contrast is between lemurids (with the exception of the bamboo specialists) with very short transit time, and the indriids with long transit time (Campbell et al., 2004).

This suggests that if one can reconstruct extinct species as primarily frugivorous or primarily folivorous, one can estimate their potential for seed dispersal. Many characteristics of the Archaeolemuridae point to a key ecological role as predominantly frugivorous seed predators and hard-object processors. Especially when combined with omnivory (as in *Cebus apella* or *Daubentonia madagascariensis*), hard-object processing allows individuals to gain access to high-quality foods that are otherwise unavailable. As reviewed above, *Archaeolemur* and *Hadropithecus* had robust jaws and dental architectural features characteristic of hard-object feeders. Coprolites of *Archaeolemur* demonstrate omnivory. Evidence for high encephalization and relatively slow dental development supports the inference that the archaeolemurids depended on complex extractive foraging; high encephalization is characteristic of extractive foragers and correlated with prolonged maternal investment. If the archaeolemurids did indeed have "high-quality" diets, then it is also likely that they had relatively short gut retention, which may have increased their effectiveness as seed dispersers, despite their propensity for seed predation.

The other extinct lemurs were probably either highly destructive to seeds or rarely consumed them at all. The Megaladapidae, as specialized folivores, would have consumed them only incidentally. We hypothesize that the Palaeopropithecidae (as predominantly folivorous seed predators) were also destructive to seeds, as are their closest living relatives, the Indriidae, or their ecological vicars on continental Africa and Asia, the colobines. Indriids today are *physiological* folivores. Some do consume a lot of fruit, but they tend to consume unripe fruits whole. They also deliberately extract and masticate seeds to the point that the seeds are virtually never distinguishable in feces (Hemingway, 1996; Ralisoamalala, 1996; Dew and Wright, 1998; Overdorff and Strait, 1998; Ganzhorn et al., 1999). Occasional intact seeds

(generally small ones; see Dew and Wright, 1998) suffer prolonged fermentation due to slow gut transit time, which may compromise the probability of successful germination. Colobines are similarly destructive to seeds; cercopithecines and particularly apes are far better seed dispersers (Davies, 1991; Peters, 1993; Wrangham et al., 1994; Lambert, 1999; Dominy and Duncan, 2005).

Summary and Conclusions

In summary, a simple picture is beginning to emerge from the combined analysis of life history profiles and trophic adaptations of extinct lemurs. It is one that has parallels in other regions of the world. We agree with Bollen et al. (2004b) that the nearly exclusive dependence of some larger-seeded trees on the remaining large-bodied lemurids today is likely a byproduct of the extinction of larger, frugivorous birds and lemurs, and that megafaunal extinctions have indeed put the largest-seeded trees in jeopardy. To this, we add the following observations:

First, within the Order Primates at least, the benign-frugivore guild on Madagascar was not much larger in the past than it is today, including only two additional members – the two species of the genus *Pachylemur*. However, there is excellent reason to believe that these species played a pivotal role in large-seed dispersal, and that their disappearance is having an adverse effect on Madagascar's forest regeneration.

Secondly, Madagascar had a large number of specialized primate folivores in the past, just as it is does today. The high percentage of primate folivores on Madagascar today is not an artifact of recent extinctions.

Thirdly, Madagascar did have many mixed feeders (large-bodied folivore/frugivores), including most of the palaeopropithecids – close relatives of indriids with similar developmental profiles and microwear signaling similar diets. High folivory in sloth lemurs is also suggested by their high shearing capacity. The largest-bodied extinct lemurs belonged to this guild, which suffered a decline in the recent past. The extent to which the extinction of these species adversely affected seed dispersal is unknown. If, in fact, palaeopropithecids were physiological folivores, it is likely that they had slow gut transit times, and were similarly destructive to seeds.

However, there existed a guild of large-bodied frugivore/omnivores that suffered an even-more-major decline, and that, we believe, did play a critical role in the long-distance dispersal of large seeds. These were Madagascar's hard-object processors, including the archaeolemurids and daubentoniids. These species had jaws powerful enough to crush the hardest foods, or they had other means (chisel-like incisors) of gaining access to well-protected resources. The combination of omnivory and exploitation of hard or protected plant parts likely allowed year-round access to high-quality foods. These species were apparently able to maximize quality-resource use even in forests with low

productivity and during the least productive times of the year. That access came with a price, however: prolonged maternal investment.

Within this guild, the archaeolemurids were almost certainly less destructive to seeds than the specialized daubentoniids. There is also strong evidence that members of this guild targeted different plant and/or animal species; they exhibit very different stable carbon isotope signals even where sympatric. *Hadropithecus* was the single lemur (extinct or extant) with a distinct (though likely not exclusive) preference for CAM or C4 plants, and/or for animals consuming such plants. The ecological roles assumed by the Archaeolemuridae would have been comparable to those served by large-bodied cercopithecines, apes and elephants in the Paleotropics, or by peccaries and capuchins in the Neotropics.

Finally, there are indeed tree species in Madagascar that appear to have been orphaned by the recent disappearance of Madagascar's megafauna. A more thorough review of possible ecological anachronisms (especially large-seeded trees with adaptations for endozoochory) is warranted. In addition, ecological investigations of the dispersal and recruitment patterns of Madagascar's large-seeded flora will elucidate their reproductive strategies and more clearly reveal which species may be suffering most from recent faunal extinctions. This information will contribute not merely to our understanding of past changes in Malagasy ecosystems, but to preventing further extinctions and ecological disruptions in the future.

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